Biomechanical and Behavioral Determinants of Flapping Frequency in Cliff Swallows

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Senior Honors Thesis

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April 3, 2020

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Abstract

One of the central predictions of applying aerodynamic theory to the flapping flight of birds and other animals is the quadratic relationship between wingbeat frequency and airspeed. This relationship has been observed in theoretical models of flapping flight and experimental studies of birds and bats flying in wind tunnels. The U-shaped curve arises from the varying power requirements for producing lift and overcoming drag at different air speeds. Because changes in wingbeat frequency have the most scope for varying muscle power output, the U-shaped cost of flight relationship is expected to lead to a U-shaped wingbeat frequency curve in all flying birds. However, the degree to which these U-shaped relationships are characteristic of natural flight behavior and the extent to which birds might modify this basic aerodynamic response to accommodate other behaviors are less well-known. We analyzed videos of wild Cliff Swallows (*Petrochelidon pyrrhonota*) engaged in tandem (i.e., following or being followed by a conspecific) and non-tandem flight behavior to collect birds' wingbeat phases and 3-D position, velocity, and acceleration through time. These data were used to determine the relationship between wingbeat frequency, air speed, and other kinematic properties such as elevation gain and centripetal acceleration. After accounting for the Cliff Swallow's intermittent flapping flight style, we found that non-tandem birds had a wingbeat frequency-speed relationship consistent with theoretical models and wind tunnel experiments, though they typically did not fly at speeds faster than the minimum-frequency speed. Cliff Swallows engaged in tandem flight behavior flew with higher wingbeat frequencies that did not vary systematically with speed, contrary to aerodynamic expectations. They also reached faster flight speeds than were seen in non-tandem behavior. These results support the applicability of the predicted wingbeat frequency-speed model to natural flight, but also show that birds can substantially modify this underlying pattern to support different flight behaviors.

Introduction

Flight is the most energy-efficient mode of terrestrial locomotion, requiring ~ 10 times less energy per unit kilogram per unit distance than walking or running while also being nearly an order of magnitude faster (Biewener et al., 2018). Since birds have a natural capacity for this cheap mode of locomotion, studying their metabolic, muscle and aerodynamic power requirements has been of interest in both fields of biology and aeronautics. Birds exhibit a large diversity in flight behaviors between species, developing specialized wing shapes and flapping styles to accommodate various ecological requirements from sustained hovering to long distance migration. The resulting variety in flapping styles and behaviors provides an opportunity to study the function and efficiency of varying flapping wing aerodynamics. This information could also improve our understanding of the biomechanical requirements for flight and thus the energetic requirements of ecologically relevant bird behaviors such as migration and foraging.

One of the most influential theories of avian flight biomechanics has been the consistent quadratic relationship between birds' mechanical power and their flight speed. This U-shaped power curve arises due to variation in power requirements needed to meet aerodynamic costs that change with speed. At lower speeds, birds have to increase their power output to produce sufficient lift forces while overcoming the induced drag, which is high due to the decreased volume of air flowing past their wings. At faster speeds induced drag declines while other drag components, such as parasite drag on the body itself and profile drag on the wings, increase with the square of speed, requiring a higher power output at high speeds (Rayner, 1999; Pennycuick, 2008). At intermediate speeds, induced drag and body (i.e. profile and parasite) drag are both low, producing a dip in costs and a characteristic U-shape. The U-shaped power to speed relationship is grounded in the fundamental physics of flight, generally consistent across species, and has been measured through various wind-tunnel studies. These studies controlled airspeed and measured the birds' mechanical power output through metabolic and pectoralis muscle power measurements, both of which showed a quadratic relationship with speed (Tucker, 1968; Tobalske, 1995; Pennycuick et al., 1996; Dial et al., 1997; Hedrick et al., 2003). Birds modulate power output

through their wingbeat frequency, either directly or through intermittent pauses within flapping flight at a muscularly optimal 'operating frequency' (Pennycuick et al., 1984). Because change of flapping frequency provides a direct means of simultaneously varying muscle and aerodynamic power, mathematical formulas have been developed for determining wingbeat frequency from a bird's physical properties and air properties (Pennycuick, 1996). Such models can be inconsistent, however - though the U-shaped power curve exists in most species, it can substantially differ in shape and placement between species based on factors unrelated to aerodynamics, such as varying flapping flight styles (intermittent vs. continuous) and behavioral effects (Rayner, 1979, 1985).

Our current understanding of these power curves predominantly comes from wind tunnel experiments. However, wind tunnel conditions can affect birds' natural flight behavior. Several such effects have been suggested, including variation in visual and acoustic cues, erratic airflows, increases in body drag from masks used for metabolic recordings, and unnatural flight speeds and styles when compared to free voluntary flight (Rayner, 1994). This project aimed to determine whether birds in their natural environment, especially birds engaged in flight behaviors other than straight and level solo flight, followed the U-shaped wingbeat frequency curve exhibited by most birds in wind tunnel studies.

For this purpose, we collected wingbeat frequency and flight speed data from birds in the field using a high-speed 3-D videography technique. We chose to study Cliff Swallows, gregarious birds that live in large colonies with nests in proximity to one another, allowing us to closely observe both flight and behavioral patterns. We expected Cliff Swallows to follow the wingbeat frequency-speed curve – though they have not been previously observed in wind tunnels, closely related Barn Swallows have exhibited the relationship, allowing for comparison between the results (Park et al., 2001). Due to their nest proximity, this species participates in intraspecific nest parasitism, which occasionally results in a flight behavior that greatly differs from regular flight (Brown et al., 1989). In this "tandem" behavior, two birds participate in a high-speed chase-like flight, which often includes complex evasion maneuvers and

occasional in-air physical fights. An earlier study of this behavior found that birds in tandem flight have an increased wingbeat frequency, hypothesized to allow for a lower reaction latency to accommodate the quick maneuvers necessary to better evade or follow the other bird in a tandem pair (Shelton et al., 2014). Because these birds appear to prioritize high wingbeat frequency for non-aerodynamic reasons, we predicted that they would not alter their wingbeat frequency over speed, and would not follow the U-shaped wingbeat frequency – speed relationship. However, we expected that Cliff Swallows not participating in tandem flights should follow the aerodynamically-predicted U-shaped curve for flight efficiency, as previously documented in closely-related Barn Swallows.

Methods

Data Collection

We analyzed videos of a Cliff Swallow colony to collect wingbeat and kinematic data. These videos were recorded by Shelton et al. at a North Carolina Highway 751 bridge over Jordan lake (35°49′42″N, 78°57′51″W). A Cliff Swallow colony of approximately 60 adults nests underneath the bridge from May – August of each year. The field videos were recorded from 3 cameras (IDT NR5-S1 model) at a frequency of 100 Hz (Fig. 1). All cameras were calibrated by passing an object of known length through the shared viewing volume, enabling measurement of the birds' 3-D trajectories (Theriault et al., 2014). Videos were collected on 13 different days in 2012 and 2013 (Table 1).

Recording Day	Total Number of Trajectories	Tandem Trajectories	Non-Tandem Trajectories
05-07-2012	2	2	0
06-14-2012	19	2	17
06-15-2012	20	2	18
06-18-2012	20	2	18
06-19-2012	41	4	37
07-05-2012	6	0	6
07-06-2012	2	0	2
05-13-2013	8	0	8
05-14-2013	12	6	6
05-16-2013	17	4	13
05-17-2013	7	2	5
05-28-2013	7	2	5
05-29-2013	9	4	5

Table 1: Recording days and number of tracks collected.

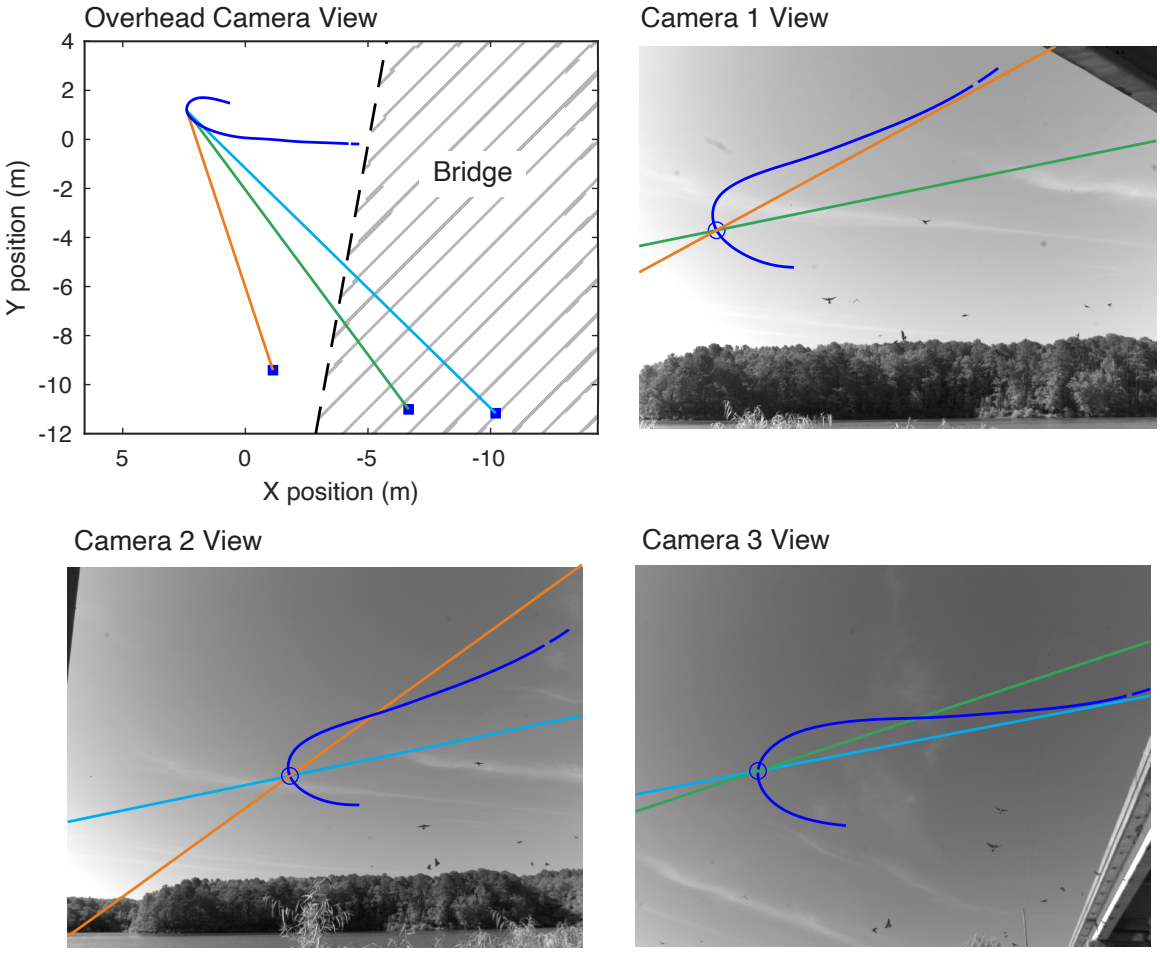

Figure 1: Camera Setup at Jordan Lake Field Site. An overhead view of the experimental setup is shown in the top-left panel. Three cameras, represented by squares, are shown at varying locations near the colony, along with each camera's line of sight extending towards a point in an example trajectory of a bird (dark blue). The following three panels show the view of a bird's trajectory through each of the cameras, and include the lines of sight of the other two cameras in the setup.

Kinematic Analysis

We used DLTdv, a video annotation tool, to analyze and compile three-dimensional positions of individual birds recorded (Hedrick, 2008). To obtain 3-D positions of tandem birds, we referred to previous manual tracking coordinates from Shelton et al., 2014. For non-tandem bird 3-D positions, we created a custom automatic tracking software that allowed us to rapidly process tracks from many birds. The software analyzed videos through two different approaches depending on the scene. The first approach was motion-driven, separating moving pixels, such as birds, from immobile background pixels

(i.e. plants, lake water, sky, and the bridge). The second approach was contrast-driven, separating birds as dark contrasting points from a light background such as the sky. The software tracked the center point of each bird frame-by-frame, and recorded position coordinates in each of the three cameras' 2-D view. We compiled these position coordinates across three cameras to create the 3-D position data with x, y, and z components. Lastly, we combined the 3-D position data across frames to give a 3-D position time series (or trajectory) for each bird. We smoothed the trajectories with a low-pass filter (3 Hz) to remove the effects of digitizing error and the high-frequency components of flapping. Using the smoothed trajectories, we derived other kinematic properties of the individual birds' flight, including speed, acceleration, flight angle, kinetic and potential energy, rate of change of kinetic and potential energy, and centripetal force (see below).

These formulas were used in calculation of kinematic inputs for general and statistical analysis from collected x, y, and z axis position data.

1. Speed (v)
   (m/s)
   [Δs = displacement in meters; t = change in time in seconds]

$$v = \frac{\Delta s}{\Delta t}$$

2. Acceleration (a)
   (m/s^2)
   [Δv = change in speed in meters per second]

$$a = \frac{\Delta v}{\Delta t}$$

3. Flight angle (θ)
   [v_z = vertical speed; v_{xy}= horizontal speed vector of components v_x and v_y]

$$\theta = \tan^{-1}\frac{v_z}{v_{xy}}$$

4. Kinetic power (K), i.e. the rate of change in kinetic energy, normalized to body mass
   (W/kg)

$$K = \frac{v^2}{2}$$

5. Potential power (U), i.e. the rate of change in potential energy, normalized to body mass (W/kg)

$$U = -9.81 v_z$$

6. The instantaneous radius of curvature (r), was computed as follows to enable calculation of centripetal force (m)

$$r = \frac{|v|^3}{\sqrt{|v|^2|a|^2 - (v \cdot a)^2}}$$

7. Centripetal force (a_c) (body weights)

$$a_c = \frac{v^2}{r}$$

Wingbeat Frequency Analysis

To record wingbeat frequency for both tandem and non-tandem birds, we manually recorded the frame number of a visually-discernable phase in the wingbeat cycle (full wing extension following upstroke). The amount of time between these frames was used to obtain the number of wingbeats per second, or instantaneous wingbeat frequency, for each individual bird. We attempted automating wingbeat frequency collection with custom software after finding good statistical agreement between automatic and manually-collected wingbeat data from non-tandem recordings. However, we found more variation in the automatic data for tandem birds, and therefore used manual phase detection to maximize the measurement quality, which was especially important for tandem flights due to the limited number of recordings (Table 1).

Data preparation

The flight kinematic and wingbeat frequency data were processed as follows to prepare them for statistical analysis, with the goal of reducing the original time series data to a set of independent samples of the instantaneous variables. Because sequential values in each flight track are highly correlated with one another, we used an autocorrelation analysis to find the shortest sampling interval that resulted in zero autocorrelation for one of kinetic power, potential power or centripetal acceleration. The track was then

sampled at this interval while also excluding any data with an instantaneous kinetic or potential power greater than 25 W/kg or less than -25 W/kg. These corresponded to instantaneous power outputs beyond the estimated maximum available aerobic muscle power and could occur either through interactions with the environment, such as a bird making a turn into a headwind, or errors in the automatic tracking routines. Making up 32% of the original dataset, these high-power values may have not been a good fit for the underlying aerodynamic models that produce the U-shaped wingbeat frequency curve in the first place, since these are based on steady-state aerodynamics.

Finally, we did not use whole-track average values because the average centripetal acceleration was close to zero in all cases. Cliff Swallows are known for their sharp turns and preliminary analysis indicated that centripetal acceleration was substantially correlated with changes in wingbeat frequency.

Using these methods, we collected at total of 195 observations from 30 tandem birds and 400 observations from 118 non-tandem birds.

Statistics

We applied linear mixed effects models to a combined tandem and non-tandem dataset, tandem-only dataset and non-tandem-only dataset to determine which kinematic properties affected wingbeat frequency. Fixed effects tested included velocity, acceleration, kinetic energy, potential energy, centripetal acceleration, the ratio of centripetal acceleration to speed, and flight angle. In each case we refined the model by dropping non-significant fixed effects and minimizing Akaike's information criterion. All calculations, including statistics, were implemented in MATLAB r2019b (The Mathworks, Natick, MA).

Results

The methods described above were successfully used to record and process 118 non-tandem and 30 tandem flights on 13 different recording days. Example tandem and non-tandem (Fig. 2) kinematic data are shown.

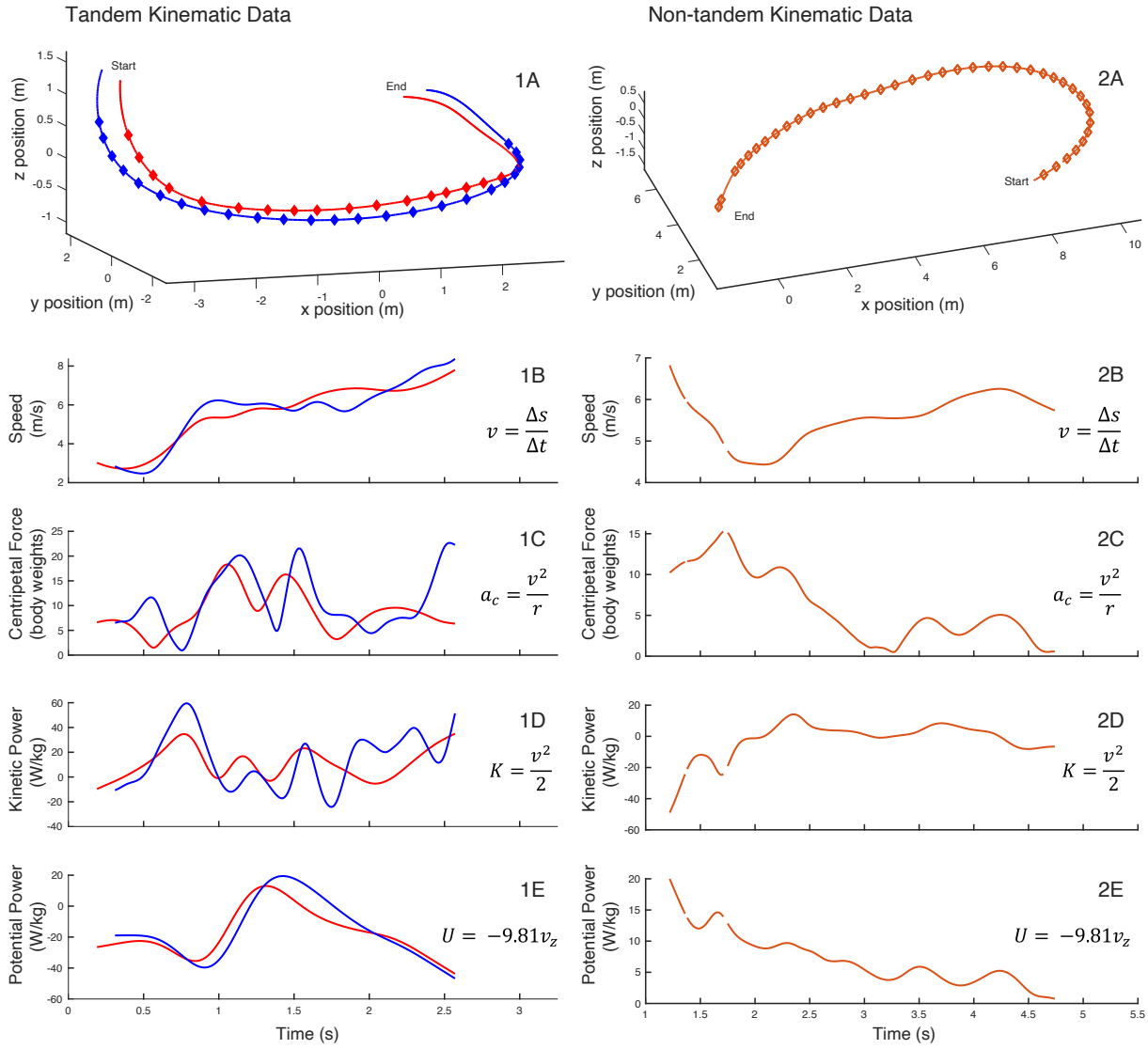

Figure 2: 3-D Position Data and Kinematic Properties of the Flight Sequence of Tandem and Non-Tandem Cliff Swallows. A 3-D trajectory was created for each bird by combining the x, y, and z position coordinates from three cameras. 1A shows an example trajectory of two Cliff Swallows in tandem flight with a diamond-marked wingbeat phase. 2A shows the same for an individual non-tandem Cliff Swallow. The position data were used to derive instantaneous speed and other kinematic properties (1B-1E for tandem, 2B-2E for non-tandem, with equations for each kinematic component) of each Cliff Swallow's flight.

We used these data to determine the kinematic variation between flight of tandem and non-tandem birds. These data were analyzed with wingbeat frequency data to determine the wingbeat frequency-flight speed relationship, and the statistical effects of kinematics on wingbeat frequency.

Distribution of observed flight speeds

Following Shelton et al. 2014, we hypothesized that participation in tandem flight behavior would alter the mean flight speed of birds, potentially differentiating it from Cliff Swallows not participating in the competitive behavior. We determined the flight speed distribution to see whether participation in tandem behavior affected the mean and range of flight speeds of birds.

We found that non-tandem birds flew at average flight speeds ranging between 2 m/s - 13 m/s. These average flight speeds were concentrated at an intermediate speed range of 5 m/s - 8 m/s, with generally few birds flying at speeds below or above of this range (Fig. 3). For tandem birds, the flight speed distribution also showed a peak at intermediate speed range, 6 m/s - 7 m/s in this case. Compared to the non-tandem birds, the tandem bird speed distribution had relatively more samples at slow and high speeds (Fig. 4).

The mean flight speeds of the tandem and non-tandem birds did not differ statistically (two-sample T test; $p = 0.79$). The modal flight speed (with 1 m/s granularity) was 6 m/s for both flight behaviors.

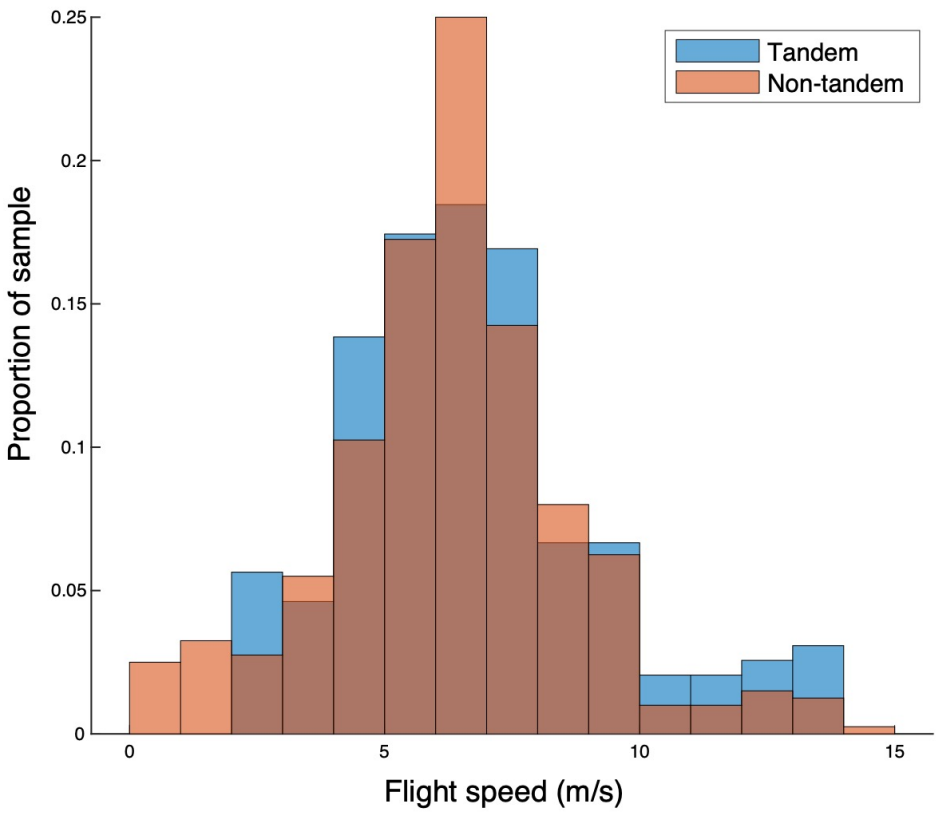

Figure 4: Histogram of flight speed distribution for the non-tandem (orange) and tandem (blue) Cliff Swallow data sets. The speed distribution shows the proportion of the tandem or non-tandem sample flying at a mean flight speed, plotted by 1 m/s intervals. The mean flight speed of tandem and non-tandem birds was statistically similar (two-sample t-test; $p = 0.79$).

Wingbeat Analysis

Without considering the effect of other kinematic parameters such as gain (or loss) of kinetic and potential energy, we found that the Cliff Swallows' participation in tandem behavior substantially affected the relationship between wingbeat frequency, flight speed, and other kinematic parameters (Fig. 5). Cliff Swallows participating in tandem flights flew at consistently high wingbeat frequencies (~11 Hz – 14 Hz) at all speeds. By contrast, non-tandem Cliff Swallows followed the expected U-shaped wingbeat frequency versus flight speed curve (Park et al., 2001). We found that these birds flew at high wingbeat frequencies while at low and high flight speeds, and decreased their wingbeat frequency at intermediate speeds (Fig. 5).

Details of flapping behavior also differed between the two behavioral groups. Cliff Swallows not engaged in tandem behavior often exhibited intermittent rather than continuous flapping flight. Gliding and partial bounds were regular components of flight, often interspersed between periods of flapping, and lasting about 150 ms on average. Tandem flight Cliff Swallows exhibited continuous flapping flight, with occasional short partial bounds (range = 20ms - 340ms).

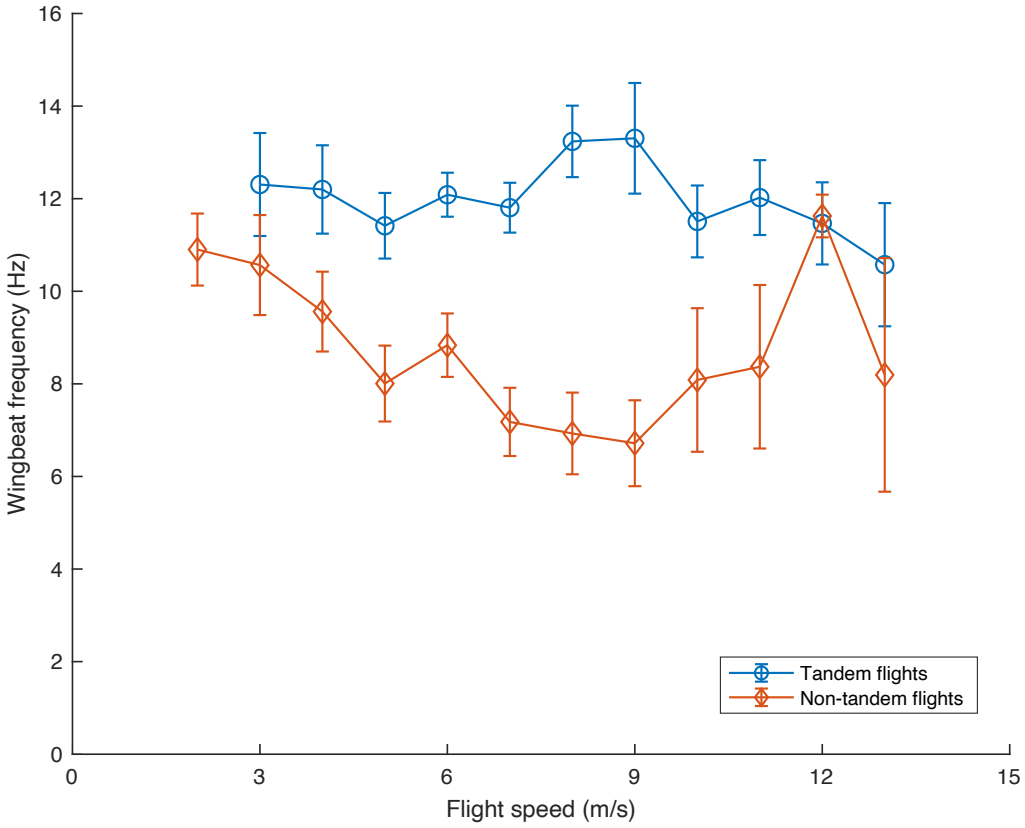

Figure 5: Wingbeat frequency versus flight speed relationship of Cliff Swallows in tandem and non-tandem flights. The mean wingbeat frequencies from instantaneous samples were averaged together and binned by the corresponding instantaneous flight speed. Error bars show standard error computed from the number of individual birds contributing data to that speed bin. These results are not corrected for behavior or other factors such as kinetic or potential energy gain (or loss) that may also affect wingbeat frequency.

Statistical Analysis

We jointly analyzed all tandem and non-tandem flight data in a linear mixed effects model with tandem flight behavior as a fixed effect, along with other likely kinematic determinants of flight speed such as speed, centripetal force, flight angle, kinetic and potential energies. In this analysis, tandem flight had

the most significant effect, demonstrating that wingbeat frequency in tandem flight behavior is significantly different from that of non-tandem behavior (Table 2). All other potential kinematic correlates were also significant but were not stratified by behavior. Because tandem flights appeared (Fig. 5) to show a different relationship between wingbeat frequency, flight speed and other kinematic measurements, we proceeded to analyze tandem and non-tandem data separately.

Formula: frequency ~ 1 + tandem + v + v^2 + a_c + K + U
AIC = 3183.3

Fixed Effects	**Estimate (Lower - Upper 95% CIs)**	**p**
tandem	3.10 (2.45 - 3.70)	1.21e-20
v (speed)	-1.12 (-1.53 - -0.71)	1.23e-07
v^2 (speed^2)	0.059 (0.031 - 0.087)	4.71e-05
a_c (centripetal force)	0.15 (0.10 - 0.20)	1.59e-08
K (kinetic power)	0.055 (0.035 - 0.075)	1.10e-07
U (potential power)	0.081 (0.057 - 0.11)	1.32e-10

Table 2: Linear Mixed Effects model analysis of the combined dataset of tandem and non-tandem behavioral and kinematic effects on wingbeat frequency, with the corresponding Akaike's information criterion (AIC) value.

We separately analyzed tandem and non-tandem Cliff Swallows' fixed effects of kinematic properties on wingbeat frequency including instantaneous samples of speed, speed squared, centripetal force, flight angle, kinetic energy, potential energy, and the ratio of centripetal force to speed. After minimizing AIC by excluding kinematic properties with little effect on wingbeat frequency, the models showed varying effects of kinematic properties on wingbeat frequencies between the tandem and non-tandem birds. Non-tandem birds' wingbeat frequency showed varying effects of all significant kinematic fixed effects on wingbeat frequency (Table 3). The positive statistical effect of v^2 (flight speed squared) on wingbeat frequency was consistent with the quadratic relationship between wingbeat frequency and flight speed (Figure 4).

Tandem birds' wingbeat frequency did not statistically vary with speed, but showed a stronger correlation with centripetal acceleration (p = 3.18 e-09); the centripetal acceleration coefficient was similar in both models.

Formula: frequency ~ $1 + v + v^2 + a_c + K + U$
AIC = 2229.2

Fixed Effects	**Estimate (Lower Upper 95% CIs)**	**p**
v (speed)	-1.23 (-1.75 - -0.70)	5.56 e-06
v^2 (speed^2)	0.061 (0.023 - 0.099)	0.0017
a_c (centripetal force)	0.12 (0.041 - 0.21)	0.0035
K (kinetic power)	0.088 (0.059 - 0.12)	3.53 e-09
U (potential power)	0.11 (0.079 - 0.15)	3.16 e-10

Table 3: Linear Mixed Effects model analysis of kinematic effects on wingbeat frequency in the non-tandem dataset, including the corresponding value of the Akaike's information criterion (AIC).

Formula: frequency ~ $1 + a_c + U$
AIC = 834.45

Fixed Effects	**Estimate (Lower Upper 95% CIs)**	**p**
a_c (centripetal force)	0.13 (0.090 - 0.17)	3.18e-09
U (potential power)	0.022 (0.0003 - 0.044)	0.047

Table 4: Linear Mixed Effects model analysis of kinematic effects on wingbeat frequency in the tandem dataset, including the corresponding value of the Akaike's information criterion (AIC).

Corrected Wingbeat Frequency Analysis

A bird's flight in wind tunnels is typically restricted to level flight without strong accelerations or changes in energy state. In order to accurately compare wingbeat frequency – speed relationships between wind tunnel and field conditions, we corrected the observed wingbeat frequency of non-tandem birds only. We corrected the data by removing the coefficients (determined from Table 3) of kinematic effects not

observed in wind tunnels, such as centripetal force, kinetic power, and potential power. Removing these effects caused an overall decrease in wingbeat frequency (Fig. 6). When plotted over speed, wingbeat frequency error bars overlapped with uncorrected wingbeat frequencies across all speeds with the exception of 12 m/s. (Fig. 6) Surprisingly, adjusting for these kinematic effects decreased the similarity between the field data (6A) and wind tunnel data (6B).

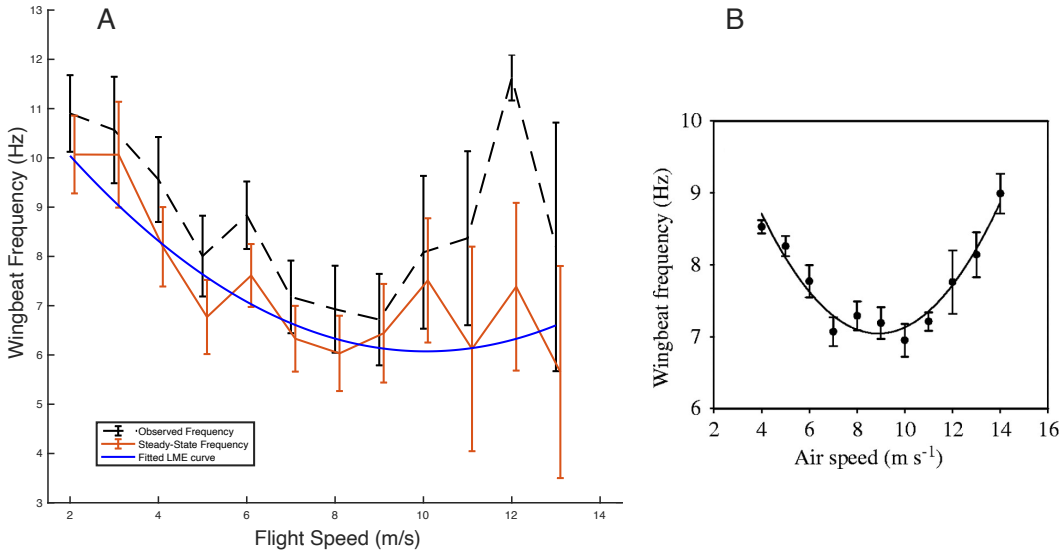

Figure 6: Comparison of Corrected Cliff Swallow Wingbeat Frequency – Speed Relationship (Panel A) to Barn Swallow Wind Tunnel Data by Park et al., 2001 (Panel B). The wingbeat frequencies of non-tandem Cliff Swallows were corrected by subtracting coefficients of centripetal acceleration, kinetic and potential energies (Table 3) multiplied by the observed values for each sample for best comparison to Barn Swallow wind tunnel results. Panel A includes fitted LME curve from speed coefficients in Table 3.

Discussion

Our field measurements of instantaneous wingbeat frequency and flight speed in Cliff Swallows supported the expected quadratic wingbeat frequency – speed relationship previously identified in wind tunnel experiments and theoretical analysis of bird flight. Unlike birds flying in wind tunnels, birds in the field voluntarily choose their flight style and can alter their speed and flapping style to achieve different goals or perform different activities. Despite this potential for variation, quadratic wingbeat frequency changes with speed occurred in the (non-tandem) field birds we observed, generally matching wind tunnel results for Barn Swallows, a related species of similar body and wing size (Park et al., 2001). However,

Cliff Swallows participating in tandem flight behavior produced an entirely different outcome and showed no significant wingbeat frequency change with flight speed. These birds presented a case where other behavioral considerations appear to override the aerodynamic efficiency considerations that underpin the prediction of a quadratic wingbeat frequency – speed relationship.

Speed Range

Cliff Swallows' speed range overlapped with the recorded air speeds of Barn swallows. Cliff Swallows flew from a range of 2 m/s to 14 m/s, with an extended lower range compared to the Barn swallows' wind tunnel speed range of 4 m/s to 14 m/s (Park et al., 2001). However, field data of birds' flight showed substantially less representation at fast speeds. Cliff Swallows in tandem and non-tandem flight behavior most often flew at speeds below 9 m/s, approximately the speed at which wingbeat frequency reaches a minimum. This suggests that the birds were more often flying close to the speed that minimizes energetic cost per unit time rather than energetic cost per unit distance. Fast flying conditions can be created and recorded easily in wind tunnels, however, these conditions may represent an upper limit of a bird's flight abilities that is not often replicated by birds in field conditions.

Intermittent flight

There has been some inconsistency in documenting wingbeat frequency of intermittent flight styles between biomechanical studies. Some studies have defined the wingbeat frequency as the observed frequency during continuous flapping phases (Pennycuick, 1996). However, some birds, including the Cliff Swallows we studied, do not use continuous flapping, and instead adopt an intermittent flight style. This flapping style involving patterned alternation between continuous flapping flight and either glides or bounding, which lengthen the duration of the upstroke to decrease wingbeat frequency and power output (Tobalske, 1995). Alternative approaches have been developed for measuring wingbeat frequency in these birds, using the average wingbeat frequency over an entire sequence of flight (Bruderer et al., 2001).

We calculated our wingbeat frequency by using the latter method, as this was the same method used for the Barn Swallow comparative study. Barn Swallows flying in a wind tunnel showed shorter intermittent flight interruptions (8-56 ms) (Park et al., 2001) when compared to Cliff Swallow intermittent flight interruptions from this study, ~ 150 ms in length. Cliff Swallows in the field likely had much more space in the air to plan and execute more extended glides or partial bounds. Furthermore, the fixed height range available in wind tunnels could limit the ability of Barn Swallows, and other birds, to interrupt their flapping without sinking to the bottom of the tunnel.

We also calculated wingbeat frequency from only continuous flapping phases, and found that this wingbeat frequency did not exhibit a U-shaped relationship with flight speed. An explanation for this result may be that Cliff Swallows in the field may exhibit some form of a "fixed gear" wingbeat frequency. The "fixed gear" hypothesis, which fits most small birds showing bounding flight behavior, states that flight muscles may operate most efficiently at an optimal downstroke frequency (Pennycuick et al., 1984). Thus, these birds modulate overall power output by varying the length of time between bursts of "fixed-frequency" wing downstrokes. Though swallows as a species are not a typical example of true bounding flight behavior, modulating power output through pauses rather than directly changing the frequency of continuous flapping would explain the variation in wingbeat frequency results between continuous flapping phases and full flight sequences.

Quadratic Wingbeat Frequency-Speed Relationship

Plotting the observed wingbeat frequency of non-tandem Cliff Swallows over their flight speed followed a U-shaped relationship. This curve was less pronounced past the speed of 9 m/s, as few non-tandem birds flew above this speed, resulting in large standard error values. However, at the most commonly observed speeds of Cliff Swallow flight (below 9 m/s), the wingbeat frequency showed a consistent decrease with increasing flight speed. A U-shaped wingbeat frequency – speed curve suggests that a U-shaped power curve is possible in the field. However, the curves may differ outside of this general

shape, as previous studies comparing wingbeat frequency to more direct power output measurements have shown that the location of the minima can vary between the two curves (Hedrick et al., 2003).

In the field, Cliff Swallows were observed diving, turning, and accelerating in ways that are not possible in wind tunnels. In order to produce the most accurate comparison of wingbeat frequency – speed curves between the wind tunnel and the field, we corrected wingbeat frequencies in non-tandem birds to remove the statistical effects of acceleration and energy gain or loss. However, we could not determine a specific comparison of minima due to the limited number of swallows flying faster than 9 m/s. There were also differences in the wingbeat frequencies observed at low and high speeds – Cliff Swallows' corrected wingbeat frequencies were slightly lower than Barn Swallows' at low flight speeds, and did not follow the expected trend at high flight speeds. This effect might be due to the use of a linear model to estimate the effect of kinetic and potential power as well as centripetal acceleration on wingbeat frequency. These relationships may be non-linear, making our statistical result a poor fit at higher flight speeds.

Behavioral Effects

We observed Cliff Swallows in tandem flight as an example of behavior that could affect the birds' preference for efficient flapping flight over other considerations. Our results supported previous observations of consistently high wingbeat frequencies in tandem flight birds (Shelton et al., 2014). The average wingbeat frequencies differed from non-tandem birds by 2 Hz - 6 Hz, and stayed at values between 11 and 14 Hz regardless of flight speed. The increased wingbeat frequency could be attributed to decreased reaction latency (Shelton et al., 2014). Since each wingbeat presents an opportunity to accelerate or change direction, Cliff Swallows in tandem flight may prioritize increasing the frequency of these opportunities at all speeds, regardless of the possible energetic consequences.

The U-shaped power curve exists due to the varying power requirements for efficient flight at different speeds. Our observations suggest that, in the alternative case of tandem flight (or other behaviors that prioritize high wingbeat frequency), the birds may not follow an "efficient" power curve at all, and that behavioral effects can override aerodynamic efficiency. This pattern is likely not exclusive to Cliff

Swallows species or the tandem flight behavior. Tandem flights show a case of noticeable wingbeat increase and change in flight style – however, there are likely other behaviors that can alter wingbeat frequency from the optimal range for additional benefit. Homing pigeons have been observed increasing their wingbeat frequency by ~1 Hz when flying in pairs to a designated home base. While this increase can be inefficient aerodynamically, flying in pairs remains beneficial for better navigation, thus reducing the amount of time needed to return home and neutralizing the cost of aerodynamic inefficiency (Taylor et al., 2018). Wingbeat frequency changes affect flight in larger, cluster-like flocks – pigeons flying in these flocks increase their wingbeat frequency up to 0.1 Hz with increased flock density. These increases were also suggested to be beneficial for the purposes of navigation and predator evasion at the cost of aerodynamic inefficiency (Usherwood et al., 2011). Following our results, both these pigeon studies might also be interpreted as a requirement for birds to place slightly more emphasis on reaction time and maneuverability when flying near other birds, even in a cooperative instead of competitive context. Though tandem flights in Cliff Swallows can result in substantial energy loss through inefficient flight, this form of intraspecific competition can also lead to increased benefits through social dominance or reproductive success (Petrie et al., 1991).

By contrast, non-tandem Cliff Swallows may not receive much benefit from changing wingbeat frequency from the aerodynamically efficient U-shaped curve, and therefore follow this relationship. Non-tandem Cliff Swallows could still engage in other energy-demanding behaviors (i.e. foraging) that may affect wingbeat frequency, but likely not to the same extent as tandem flight which appears to directly favor high frequency (and thus low latency) flapping.

Future studies

Our study primarily analyzed wingbeat frequency over intermittent flight, finding that this measurement showed closer results to a U-shaped wingbeat frequency-speed curve than wingbeat frequency in continuous flapping sequences. There is some discrepancy between these results and earlier evidence that small passerines such as swallows do not exhibit a “fixed gear” flapping style (Tobalske et al., 1999,

2005). This intermittent flight style was more commonly observed in the field than in wind tunnels, and warrants further study analyzing its relationship to wingbeat frequency-speed curves.

It is also unknown how bird flight and wingbeat frequency in the field can be affected by more complex aerodynamic effects, such as flight into a headwind or tail wind. These effects can be difficult to imitate in wind tunnels, but are commonly encountered in the field, and could be analyzed further to understand natural aerodynamic obstacles of avian flight.

Lastly, video analysis is currently the primary means of detecting flapping events of birds in the field without attaching transmitters or accelerometers directly to birds. While our methodology was the most accurate option available to us in video analysis, manual selection of flapping events was time-consuming. In order to increase the volume of birds included in the analysis, we developed an automatic wingbeat frequency detection system that accurately reported wingbeat frequencies of non-tandem birds but contained too many errors to be suitable for use of the fewer tandem flight recordings. Further development of wingbeat-frequency recording software for video analysis could increase the amount of information available for understanding wingbeat frequency trends in unrestrained field birds.

Acknowledgments

I would like to thank Hedrick lab alumni Ryan Shelton and Brandon Jackson for recording the Cliff Swallow data sets used for this project, and Aaron Corcoran for helping develop automatic position and wingbeat frequency tracking. I would also like to thank members of the Hedrick Lab and the Biology Thesis class for their feedback and contributions to the clear communication of my results. Finally, I would like to thank Dr. Tyson Hedrick for mentorship in writing and developing the experiment.

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